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## The Identity of *Doris* (*s.l.*) Species MacFarland, 1966 (Mollusca, Nudibranchia, Discodorididae): A Persistent Mystery from California Solved

by

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The Californian dorid nudibranch species, previously referred to by several authors as *Doris* (*s.l.*) species, based upon its original reference in MacFarland (1966), is a synonym of *Diaulula sandiegensis* (Cooper, 1863). The single specimen examined by MacFarland, and other animals collected from southern California, matching the external coloration of *Doris* (*s.l.*) species, have been examined and their internal anatomy is identical to that of *Diaulula sandiegensis*. Some variation has been observed in the shape of the outermost radular teeth of this species. The obscure and poorly described species *Doris odonoghuei* Steinberg, 1963 (= *Doris echinata* O'Donoghue, 1922) is probably a synonym of *Diaulula sandiegensis* as well.

The monographic work “Studies of the Opisthobranchiate Mollusks of the Pacific Coast of North America” by F. M. MacFarland was published posthumously in 1966. This work is composed of a series of unpublished notes that MacFarland had been preparing at the time of his death. One of several of the undescribed species included was referred to as *Doris* (*s.l.*) species. MacFarland frequently used Latin abbreviations in his notes and manuscripts, and in this instance “s.l.” referred to the Latin, *sensu lato*, in the broader sense. MacFarland (1966) did not provide a specific name for this animal, which has similar external morphology and coloration to *Diaulula sandiegensis* (Cooper, 1863). He examined only one specimen of *Doris* (*s.l.*) species (Fig. 1), collected from Arch Rock Pool, Newport Bay, California, but he never studied it anatomically. The name *Doris* (*s.l.*) has been carried in the literature in numerous publications (Sphon and Lance 1968; Behrens 1980; McDonald and Nybakken 1981; McDonald 1983), and it is normally used for dorid nudibranchs similar to *Diaulula sandiegensis* but having pale dorsal spots. Other authors referred to this animal as *Doris* sp. (McDonald and Nybakken 1981; McDonald 1983) or *Diaulula* sp. 1 (Behrens 1991, 1992). All these references are based on MacFarland’s descriptions and newly collected specimens as well. However, the question of whether this animal constitutes a different species from *Diaulula sandiegensis* remains unresolved.

Prior to the publication of MacFarland’s (1966) memoir, a species with similar external characteristics was described as *Doris echinata* by O’Donoghue (1922). Later, Iredale and O’Donoghue (1923) reassigned this species to *Doridigitata* d’Orbigny, 1839 and changed the name (without explanation) to *Doridigitata maculata*. Steinberg (1963) noted that both O’Donoghue’s names were preoccupied by *Doris echinata* Lovén 1846 and *Doris maculata* Garstang 1896, respectively, and proposed a new name, *Doris odonoghuei* for this species. Additionally, Steinberg (1963) questioned whether

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the placement of this species in the genus *Doris* is accurate and suggested that further study was necessary.

In this paper we attempt to determine the identity of *Doris* (*s.l.*) species based on the study of MacFarland's original material and additional specimens deposited at the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ). In addition, the status of *Doris odonoghuei* is discussed.

## MATERIAL AND METHODS

For this paper several species matching the external coloration described for *Dialula sandiegensis* and *Doris* (*s.l.*) species were examined. Table 1 summarizes the material sources and collection localities. Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a dissecting microscope using a camera lucida. Parts of the dorsum have been critical point dried for scanning electron microscopy (SEM) of the caryophyllidia. Special attention was paid to the morphology of the reproductive system and digestive system, including the radulae, which have been prepared for examination on SEM. Features of living animals were recorded from photographs or notes of collectors.

## DESCRIPTIONS

**EXTERNAL MORPHOLOGY.**—The living animals measured up to 53 mm in length. The background color varies from translucent white to tan (Figs. 1; 2A, B). The notal surface is covered with brown specks and bears numerous irregular oval brown spots. In most specimens the center of the brown spots is lighter in color, surrounded by a dark ring. A white band, composed of minute white specks occurs along the notal margin. The body is oval, highest along its midline, sloping gradually to the margins. The notal surface is densely covered with various sized caryophyllidia (Fig. 3D). The gill is completely retractile into a branchial pit. The six tripinnate branchial leaves are upstanding and do not spread to the edges of the notum. The branchial leaves are white to cream in color and are densely sprinkled with brown specks. The anal papilla is located at the center of the branchial plume. The rhinophores are perfoliate with 12–18 lamellae and are retractile into short upright sheaths. The color of the rhinophores is similar to that of the branchial plume. Ventrally, the foot is grooved and notched, wide, tapering posteriorly into a round end. The posterior end of the foot extends only slightly beyond the posterior margin of the notum. The oral tentacles are slender and pointed distally (Fig. 5C).

**ANATOMY.**—The labial cuticle is smooth. The radular formula is  $14 \times 16.0.16$  in a 10-mm-long specimen (CASIZ 060977),  $15 \times 23.0.23$  in an 18-mm-long specimen (CASIZ 025880) and  $22 \times 27.0.27$  in a 46-mm-long specimen (CASIZ 068277). There is no trace of rachidian teeth. The lateral teeth (Figs. 3A, B; 4A, B) are simple hamate increasing in size from the center of the radular ribbon to the ninth and tenth tooth, then decreasing to the margin. The outermost two lateral teeth are very elongate and are smooth (Fig. 3C), or have one to three small denticles (Fig. 4C, D), depending on the specimen.

The reproductive system is triaulic (Fig. 5A, B). The ampulla is tubular and convoluted. It narrows into a short thin tube and connects to the oviduct and prostatic portion of the vas deferens. Immediately after branching, the oviduct enters the massive female gland mass. The vas deferens is long and slightly thinner than the ampulla, until it expands into two wide and large, contiguous prostatic portions. A long, thin duct emerges from the prostatic portion and becomes highly convoluted in the ejaculatory segment, prior to entering a common genital atrium with the vagina. The vaginal duct is thick, normally straight and connects to the large, round bursa copulatrix. A separate duct from the bursa copulatrix connects to the smaller, spherical seminal receptacle. A short, thin uterine tube

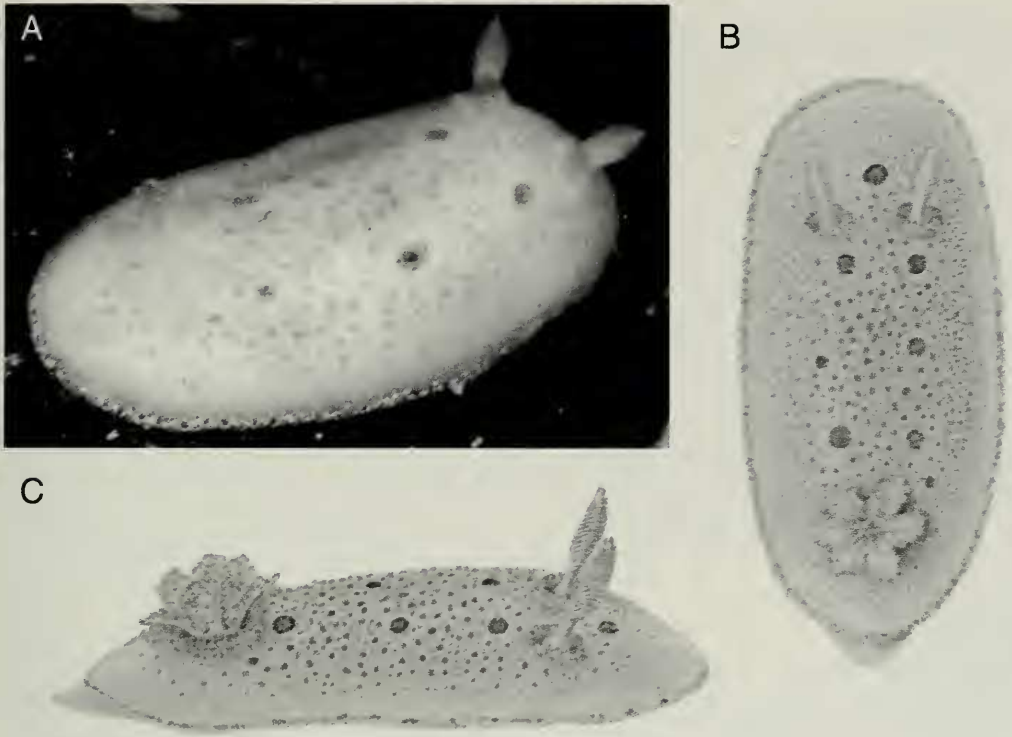


FIGURE 1. Specimen identified by MacFarland (1966) as *Doris* (*s.l.*) species (CASIZ 025880). A. Photograph of the living animal taken by G. E. MacGinitie. B, C. Drawings published by MacFarland (1966, pl. 25, figs. 1, 2).

emerges near the connection of this duct and then connects the seminal receptacle to the female gland near the genital atrium.

#### DISCUSSION

After the anatomical study of the material of *Doris* (*s.l.*) species examined by MacFarland (CASIZ 025880), of additional specimens with a similar external coloration from southern California (CASIZ 060976), and of specimens matching the original description of *Diaulula sandiegensis* (CASIZ 068277; CASIZ 071641), we were unable to find any consistent differences. It is clear that *Doris* (*s.l.*) species constitutes a color variation of *Diaulula sandiegensis*. The external coloration of this species is extremely variable. It ranges from white or cream to yellow, with brown rings or solid spots, sometimes surrounded by an opaque white ring (Fig. 2). Specimens from Canada, Alaska, and the Russian far east generally have the dorsum covered with numerous very dark spots (Fig. 2E, F), whereas in southern California and Mexico the spots are lighter and less common. Specimens from central and northern California, Oregon, and Washington match the original description by Cooper (1863).

The reproductive system of all the specimens examined has two large and distinct prostatic regions in the vas deferens. There is a long, thick, straight vaginal duct. The oviduct, vas deferens and uterine duct all enter the female gland mass in the same proximity, near the genital atrium (Figs. 5A, B; 6A, B).

TABLE 1. Sources of material examined. Specimens originally identified as *Doris* (*s.l.*) species are marked with an asterisk \*.

Locality	Date	Specimens	Length	Collector	Catalog No.
<b>Mexico</b>					
Roca Ben, Pacific coast of Baja California	20 August 1987	7	16-36 mm	T. M. Gosliner	CASIZ 071641
<b>California</b>					
San Onofre State Beach, San Diego Co.	9 December 2000	3	4-10 mm	J. Goddard	CASIZ 060977*
Bird Rock, La Jolla, San Diego Co.	10 December 2000	1	14 mm	J. Goddard	CASIZ 060976*
Paradise Cove, Malibu, Los Angeles Co.	14 September 1971	1	12 mm	S. Anderson	CASIZ 070753*
Corona del Mar Way, Orange Co.	8 May 1946	1	18 mm	F. MacFarland	CASIZ 025880*
Santa Barbara, Santa Barbara Co.	August 1966	1	15 mm	J. Steinberg	CASIZ 025785*
Virg's Landing, Morro Bay, San Luis Obispo Co.	22 November 1971	1	10 mm	G. McDonald	CASIZ 070822*
Asilomar, Monterey Co.	5 May 1973	1	7 mm	G. McDonald	CASIZ 070825
West side of Tomales Bay, Marin Co.	12 March 1961	3	21-46 mm	A. G. Smith	CASIZ 068277
<b>Canada</b>					
Round Island, British Columbia	30 May 1946	1	22 mm	E. Ricketts	CASIZ 068265

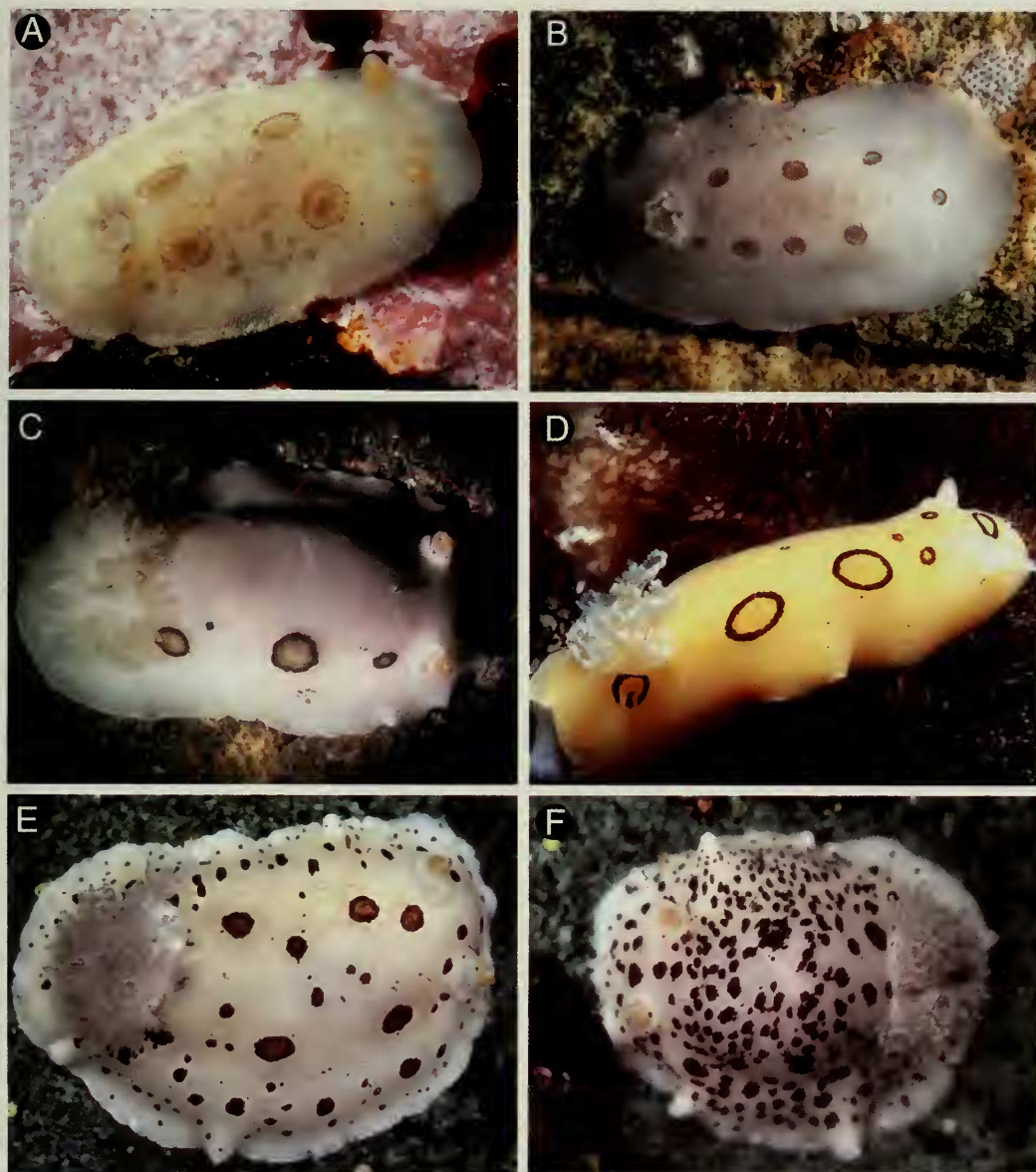


FIGURE 2. Living animals of *Diaulula sandiegensis* (Cooper, 1863). A. Specimen from San Diego, California, originally identified as *Doris* (*s.l.*) species; B. Specimen from Orange County, California, originally identified as *Doris* (*s.l.*) species; C. Specimen from San Luis Obispo, California; D. Specimen from the Channel Islands, California; E. Specimen from Vancouver Island, British Columbia, Canada; F. Specimen from Vancouver Island, British Columbia, Canada. Photograph 1A by J. Hamann, others by D. Behrens.

Camera lucida drawings based on light microscopy of the radula of *Doris* (*s.l.*) species (MacFarland 1966; McDonald 1983, 1997; Behrens 1992) suggests that the species has smooth, hamate, outer lateral teeth. Scanning electron microscopy of the specimen seen by MacFarland (Fig. 4C, D) shows the presence of denticles on the outer two lateral teeth. This character is not present in other examined specimens with the same color pattern collected from southern California (Fig.

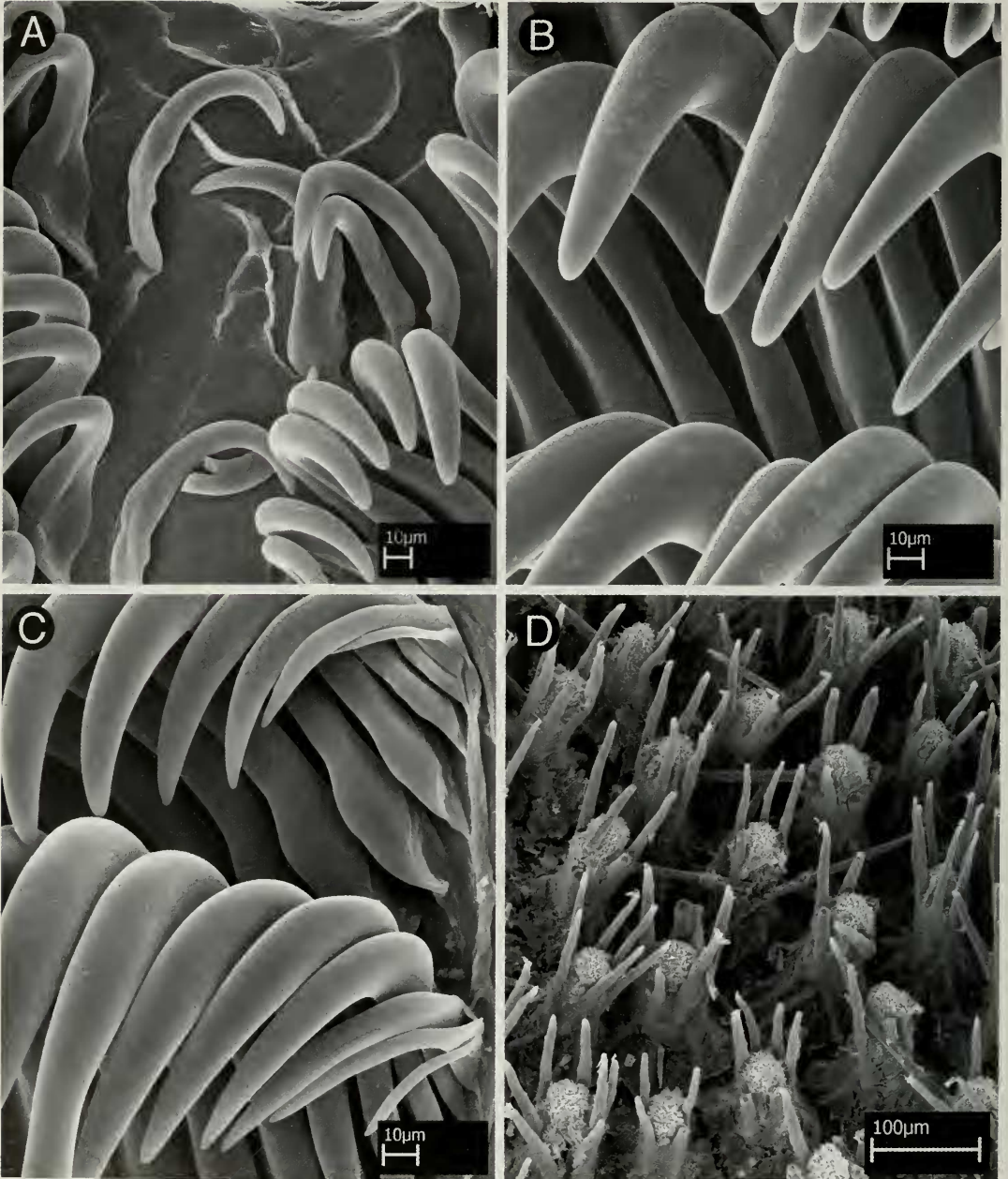


FIGURE 3. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs of a specimen originally identified as *Doris* (*s.l.*) species (CASIZ 060977). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Caryophyllidia.

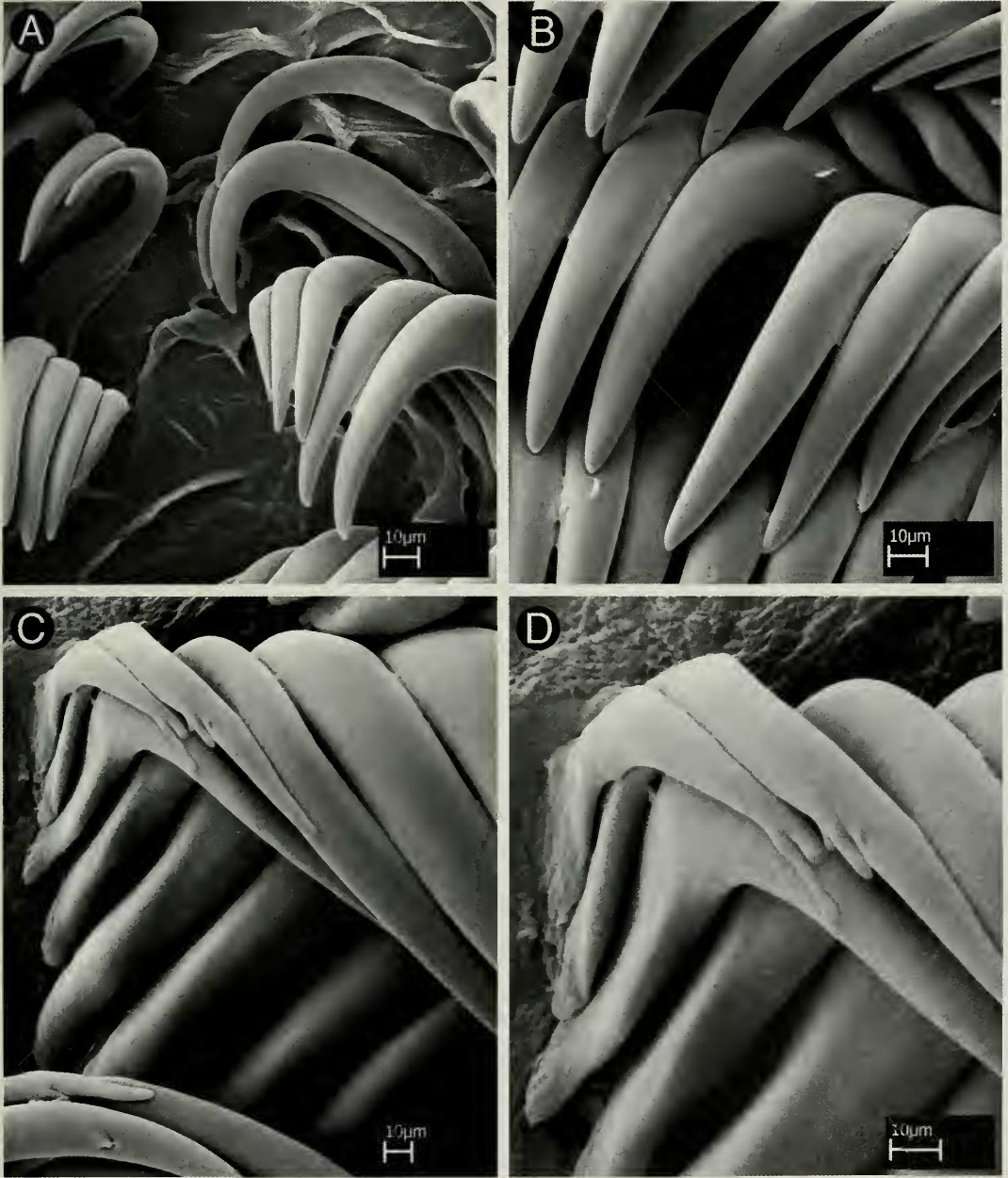


FIGURE 4. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs of a specimen identified by MacFarland (1966) as *Doris* (*s.l.*) species (CASIZ 025880). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Detail of the denticles on the outer lateral teeth.

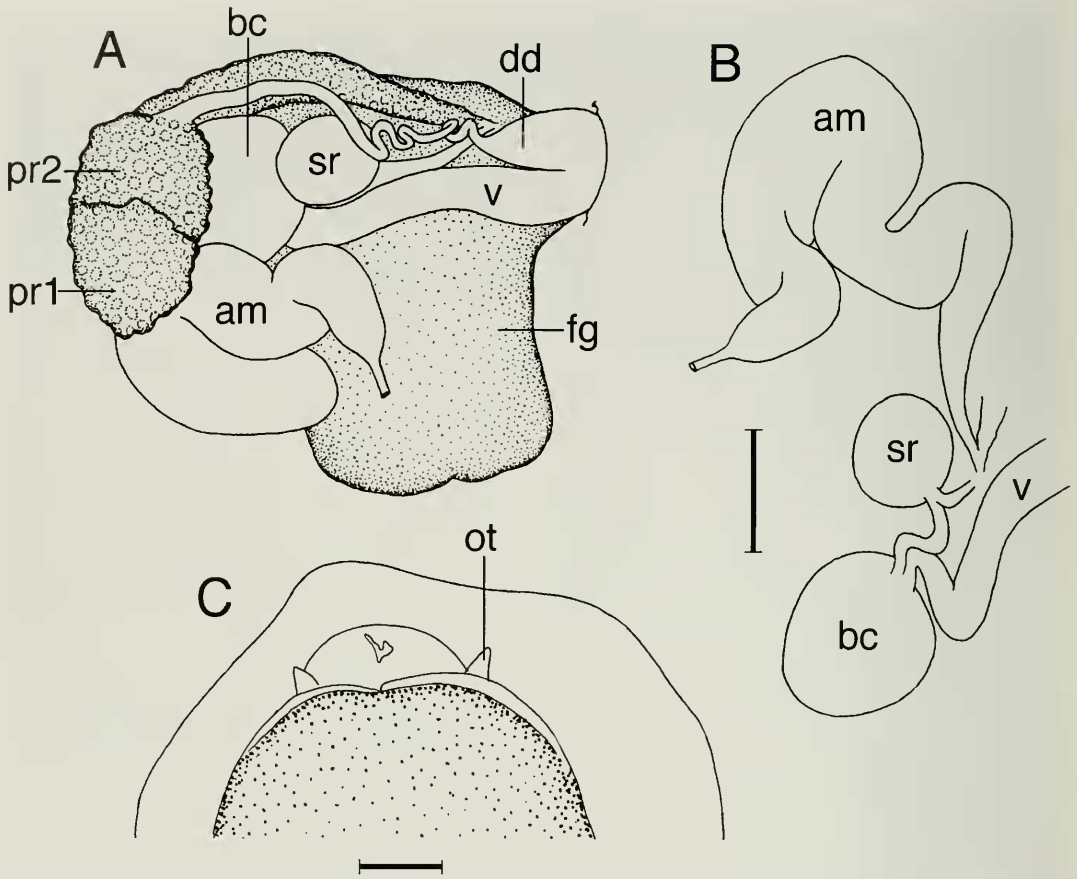


FIGURE 5. *Diaulula sandiegensis* (Cooper, 1863), anatomy of a specimen originally identified as *Doris* (*s.l.*) species (CASIZ 060977). A. Reproductive system, scale bar = 1 mm; B. Detail of several organs, scale bar = 1 mm; C. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr1, proximal prostatic region; pr2, distal prostatic region; sr, seminal receptacle; v, vagina.

3A–C), so it is clearly due to intraspecific variation. Other specimens of *Diaulula sandiegensis* have smooth, sharply-pointed, hamate-shaped teeth across the entire row (Fig. 7A–C), identical to those of *Doris* (*s.l.*) species.

Scanning electron microscopy of *Diaulula sandiegensis* clearly indicates the presence of caryophyllidia (Fig. 7D), which are identical in size and density to those present in *Doris* (*s.l.*) species (Fig. 3D).

O'Donoghue's (1922) description of *Doris echinata* was brief, stating simply that the dorsum is covered with spiculate papillae and the color is opaque white with from a dozen to forty small brown spots scattered irregularly over the surface. The radula was described as simply hamate, 16–18 rows of 13–15 lateral teeth per half-row. A description of the reproductive system is lacking, except for mention that the penis is unarmed. O'Donoghue (1922) stated that though he felt that the classification of the family was unsatisfactory, *Doris echinata* falls within its definition.

In proposing the name *Doris odonoghuei* to rectify the preoccupancy issue discussed earlier, Steinberg (1963) examined two specimens from the collection of the Friday Harbor Marine Laboratories. Questioning the assignment of the species to *Doris*, she dissected the smaller of the two, but came to no satisfactory conclusion. Recent review of her personal notes (J. Steinberg, pers. commun., Jan. 2001) revealed no further evidence to assist in its placement.



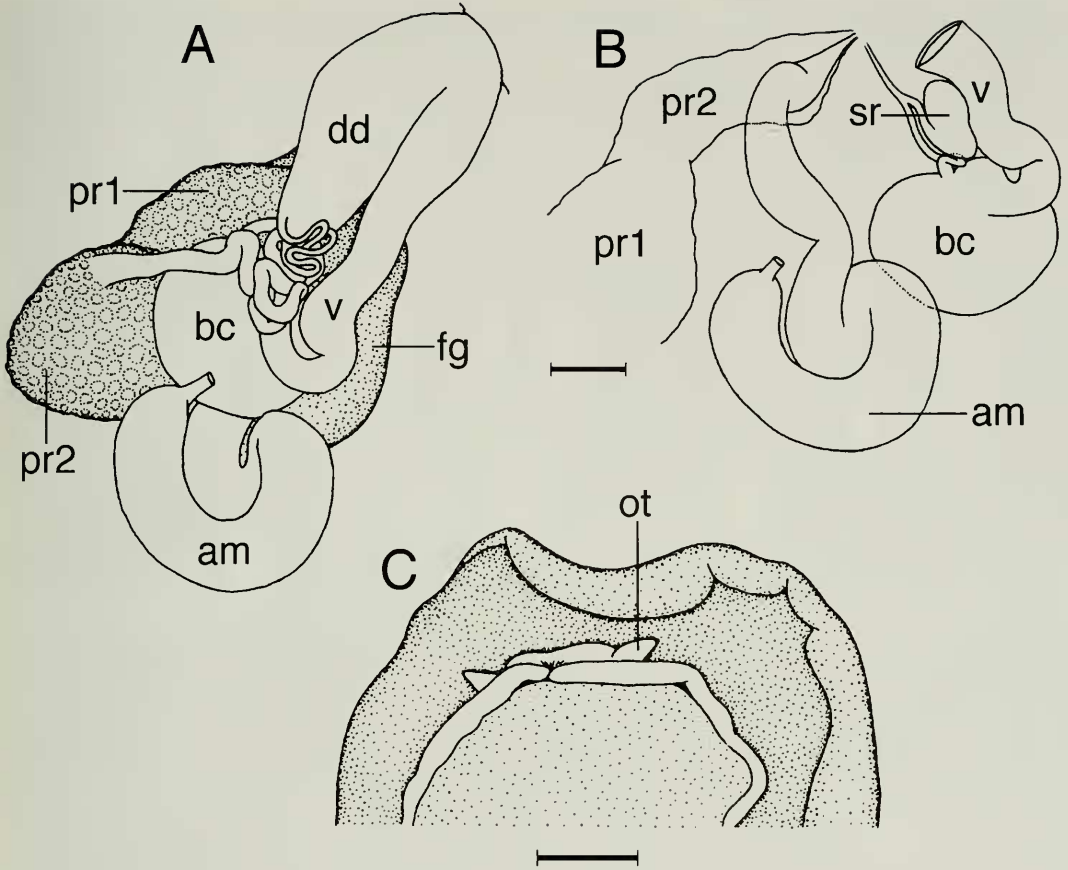


FIGURE 6. *Diaulula sandiegensis* (Cooper, 1863), anatomy (CASIZ 068277). A. Reproductive system, scale bar = 1 mm; B. Detail of several organs, scale bar = 1 mm; C. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr1, proximal prostatic region; pr2, distal prostatic region; sr, seminal receptacle; v, vagina.

Since that time no published accounts or casual observations have been made of this species. Sandra Millen (pers. commun., April 1982) indicated that she had never collected specimens in the Vancouver area, British Columbia, that she could clearly identify as *Doris odonoghuei*. According to Millen it is impossible to distinguish *Doris odonoghuei* from small *Diaulula sandiegensis*.

Whereas this species has not been definitely confirmed since O'Donoghue's (1922) original description and no type material is available for examination, and whereas this description cannot be differentiated from *Diaulula sandiegensis*, we propose that this species be regarded as a synonym of *Diaulula sandiegensis*.

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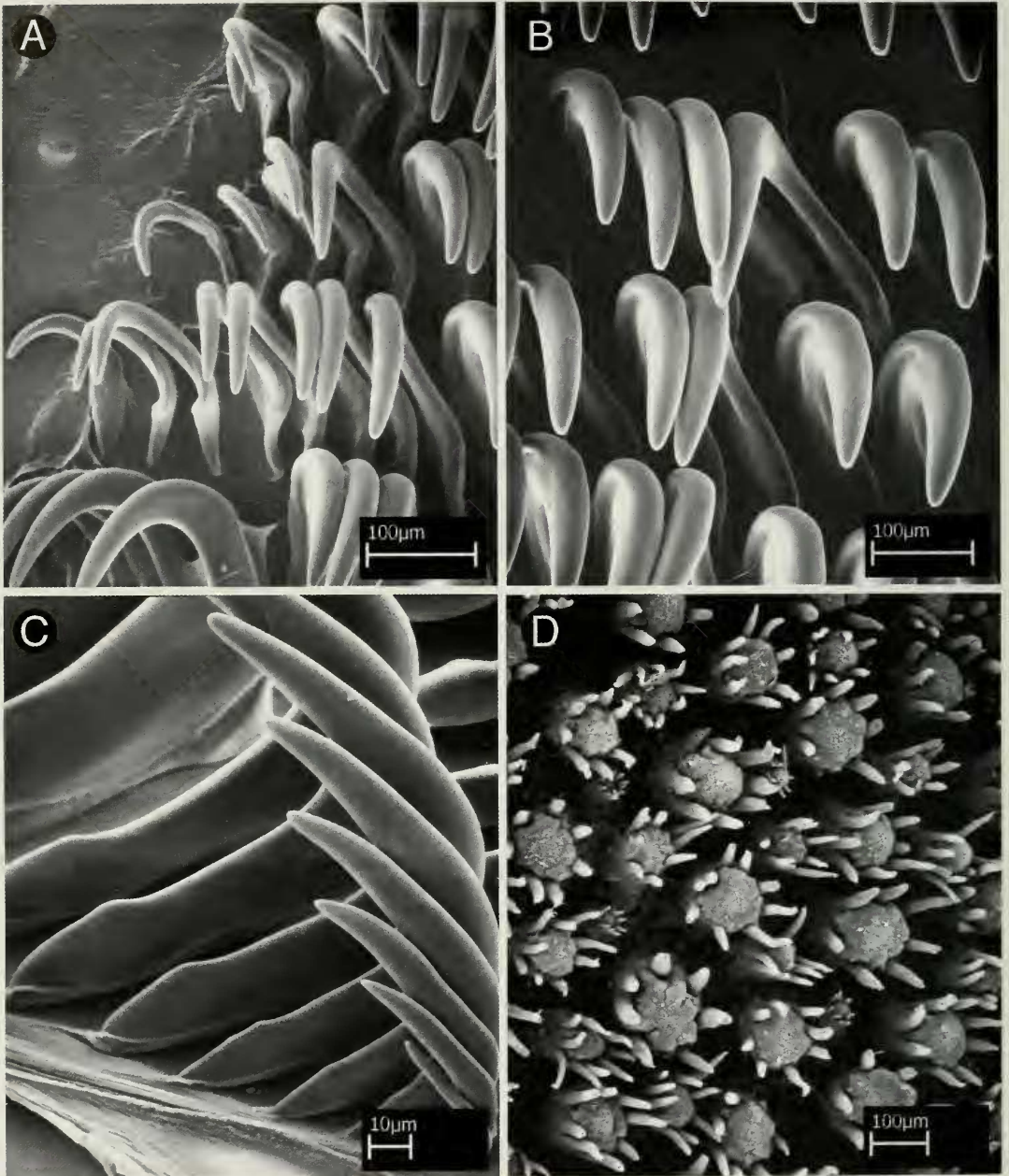


FIGURE 7. *Diaulula sandiegensis* (Cooper, 1863), scanning electron micrographs (CASIZ 068277). A. Inner lateral teeth; B. Lateral teeth from central portion of half-row; C. Outer lateral teeth; D. Caryophyllidia.

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